

**Epilimnetic Phytoplankton and Zooplankton Biomass and Species
Composition In Lake Michigan, 1983 to 1992.**

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ABSTRACT

Phytoplankton: Phytoplankton and zooplankton were collected at offshore sites of Lake Michigan during 48 cruises in the spring, summer and autumn from 1983 to 1992. For the period, 39 common phytoplankton species accounted for 84.6% of the total abundance and 87% of the biomass. Over the ten-year study period, the lake-wide average spring and summer phytoplankton biomass in the pelagic waters ranged from 0.27 to 1.2 g/m³ (mean ± S.E = 0.54 ± 0.03 g/m³) and the phytoplankton abundance ranged from 1,217 to 4,568 cells/mL (mean ± S.E. = 2,706 ± 94 cells/mL). Except for 1989, when the relative biomass of diatoms was unusually low (14.6%), relative biomass of diatoms ranged from 49.1% to 85.6% with no distinct upward or downward trend. The data support the concept of a shift in summer species composition away from blue-green algae dominance. However, considerable variability in predominance of summer phytoplankton from year to year was observed. In several years, diatoms were dominant in August as well as April.

Numerically dominant non-diatoms during the 1983-92 period included Monorhanthidium contortum and an unidentified Green coccooid (Chlorophyta), Ochromonas sp. and Chromulina sp. (Chrysophyta), Rhodomonas minuta (Cryptophyta), Anacystis montana and Oscillatoria limnetica (Cyanophyta). Cyclotella comensis, Fragilaria crotonensis, Aulacoseira italica and A. islandica were the numerically prevalent diatoms, while Stenhanodiscus alpinus, S. transilvanicus, S. niagarae, Rhizosolenia eriensis and Tabellaria flocculosa were prevalent based on biomass. Considerable yearly variability in diatom dominance occurred each year of the 10-year study. A decline in abundance of R. eriensis, R. longiseta, Cyclotella michiganiana, C. stelligera and Tabellaria flocculosa since 1962 is suggested by our data. Oscillatoria limnetica, Anacystis montana, the Haptophyceae, Chromulina sp., Ochromonas sp., Cyclotella comensis and Stephanodiscus alpinus have become more prevalent in the lake as compared to pre-1980 studies. However, O. limnetica appears to be decreasing since the early 1980s.

Mesotrophic diatoms accounted for 47.2% of the total phytoplankton biomass in the pelagic region of Lake Michigan. The lack of a trend in the ratio of mesotrophic to eutrophic diatom species suggests no change in trophic status occurred during the 1983-92 period. Considerable variability in the size composition of the spring phytoplankton community was evident with small unicellular algae predominating in 1986 and 1987 and filamentous algae

increasing to over 30% of the total biomass in 1990 and 1991. Because of the appearance and disappearance of large-bodied zooplankton over the 10-year period, the lack of any substantial changes in phytoplankton biomass and the relatively stable size composition of the summer phytoplankton was surprising. However, small unicellular algae increased from 28% to 40-50% of the total biomass after 1984.

Zooplankton:

From 1983 to 1992, 71 species representing 38 genera from the Calanoida, Cladocera, Cyclopoida, Mysidacea, Rotifera, Mollusca and Harpacticoida comprised the offshore zooplankton community of Lake Michigan. Twenty-one common species plus their juvenile stages accounted for 94.9% of the total biomass and 95.5% of the total abundance. Average density and biomass for 1983 - 1992 (spring and summer) was 91.3 organisms/L \pm 6.7 (mean \pm S.E.) and 48.0 μ g/L \pm 4.3 (mean \pm S.E.). Biomass was considerably higher in the summer (81.8 \pm 8.5 μ g/L) than in the spring (20.1 \pm 1.6 μ g/L).

Our lake-wide data not only support the contention that major changes in the Daphnia community occurred after the invasion of Bythotrephes cederstroemi but also to several other species of Cladocera and one Cyclopoida. After 1986 and the invasion of the predaceous Bythotrephes, the entire composition of the zooplankton community shifted from a broadly diversified abundant Cladocera community of ten species to only three species by 1991 and 1992 with dominance centered in one species (Daphnia galeata mendotae) that accounted for over 95% of the Cladocera abundance. A similar situation was not evident with the Copepoda. With the establishment of B. cederstroemi in 1986, the relatively large, perhaps less mobile, herbivorous species (Daphnia pulicaria, Daphnia retrocurva, Holopedium gibberum) were removed from the lake first and by 1987. By 1990 the larger and mobile predaceous Cladocera, such as Leptodora and the cyclopoid Mesocyclops edax, were eliminated followed by a slow decrease in abundance of the smaller herbivorous Cladocera (Bosmina longirostris and Eubosmina coregoni). During this period, Daphnia galeata mendotae abundance increased dramatically.

A major change in the species composition of Lake Michigan zooplankton was evident by 1990. Is it possible for Bythotrephes to be the sole cause of all the compositional changes in the pelagic zooplankton community of Lake Michigan observed, especially after 1990 when major

changes in zooplankton composition occur while Bythotrephes abundance is considerably lower than in 1989? Abundance of at least two other planktivorous feeders (Alosa pseudoharengus - alewife and Coregonus hoyi - bloater chub) increased after 1987. Our data demonstrate that the composition and abundance of the calanoid community after 1987 are not unlike that of 1960s and that the calanoids are now the dominant crustacean group as compared to the cladocerans in the early 1980s. However, the species diversity and evenness of the Cladocera community in the early 1990s is unlike anything that has been previously reported for Lake Michigan. Cladocera dominance is centered in one species, Daphnia galeata mendotae, and only three species of Cladocera were observed in the lake in 1991 and 1992.

INDEX WORDS: Lake Michigan, phytoplankton and zooplankton biomass and abundance, historical trends, eutrophication trends, food web changes.

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INTRODUCTION

Evidence of appreciable change in the biota of Lake Michigan (e.g. Jude and Tesar 1985, Evans and Jude 1986, Scavia *et al.* 1986, Fahnenstiel and Scavia 1987, Stewart and Ibarra 1991, Evans 1992) has directed attention to the long term data sets of phytoplankton and zooplankton collected by the Great Lakes National Program Office of the U.S. Environmental Protection Agency. Phytoplankton, which have short carbon turnover rates, are sensitive to water quality conditions and grazing by zooplankton, and thus respond rapidly to perturbations of the lake ecosystem. The determination of phytoplankton abundance and species composition is one method to trace long-term changes in lakes (Munawar and Munawar 1982, Makarewicz 1993, Makarewicz and Bertram 1991). Similarly, whether aquatic ecosystems are perturbed by changes in the top predator fish that cascade down the food web or by nutrients or other stressors that are expressed from the first trophic level upward, the zooplankton are sensitive integrators of such changes (McNaught and Buzzard 1973). They have also proved useful for complementing phytoplankton data to assess the effects of water quality (Gannon and Stemberger 1978) and fish populations on biota (e.g. Brooks and Dodson 1965). The large interannual variability in abundance of zooplankton requires long-term data sets to detect trends in zooplankton abundance (Evans 1992). Thus zooplankton have value as indicators of water quality and the structure of the biotic community. Specifically, has there been a reduction or other change in the phytoplankton community concomitant with the top-down mediated changes observed in the fish and zooplankton community during the 1980s? In this study, the 1983-92 spring and summer phytoplankton and zooplankton data assemblages presented make it possible to examine the historical, geographic, and seasonal relationships prevailing in Lake Michigan and to compare them, where possible, to previous studies.

METHODS

Phytoplankton

Phytoplankton were collected during 48 cruises during the spring, summer, and autumn from 1983 to 1992 (Table 1). Only data from the spring and summer are reported here. Unless otherwise noted, only the spring and summer data are presented to allow comparisons between

years. An 8-L PVC Niskin bottle mounted on a General Oceanics™ Rossette sampler with a Guildline™ electrobathythermograph (EBT) was used to collect phytoplankton. Phytoplankton samples were obtained by compositing equal aliquots of samples collected at depths of 1, 5, 10 and 20m. Since the deep chlorophyll layer does not form until thermal stratification occurs and is at a depth of 40-70m in August (Fahnenstiel and Scavia 1987), our species data represent only summer epilimnetic forms and early spring isothermal forms.. One liter samples were immediately preserved with 10 mL of Lugol's solution and formaldehyde was added upon arrival in the laboratory. The settling chamber procedure (Utermöhl 1958) was used to identify (except for diatoms) and enumerate phytoplankton at a magnification of 500x. A second identification and enumeration of diatoms at 1250x was performed after the organic portion was oxidized with 30% H₂O₂ and HNO₃. The cleaned diatom concentrate was air dried on a #1 cover slip and mounted on a slide (75x25mm) with HYRAX™ mounting medium. Replicate identifications were made by different analysts on every 10th sample and compared for consistency in species nomenclature and abundances. Precision goals between replicates were based on the Relative Percent Deviation ($RPD = ((\text{larger count} - \text{smaller count}) / \text{average}) \times 100$). For example, the precision goal for replicated Bacillariophyta counts was $\pm 15\%$. Values outside this goal were rejected and the samples recounted unless a clear explanation was available, e.g., very low abundance of forms in any one division. In addition, validation of species identifications between different enumerators over the 10-year period were made to ensure consistency in identifications. Changes in nomenclature, use of synonyms, etc are discussed in the Appendix (Table A1).

The cell volume of each species was computed by applying average dimensions for each species from each sampling station and date to the geometrical shape that most closely resembled the species form, e.g., sphere, cylinder, prolate spheroid, etc. At least 10 specimens of each species were measured from each sample for the cell volume calculation. When fewer than 10 specimens were present, they were measured as they occurred. For most organisms, the measurements were taken from the outside wall to outside wall. The dimensions of the protoplast were measured for loricated forms, while the dimensions of individual cells were measured for filaments and colonial forms. Biovolume ($\mu\text{m}^3/\text{L}$) was converted to biomass

(mg/m^3) assuming a specific gravity of 1.0 for all phytoplankton ($\text{mm}^3/\text{L}=\text{mg}/\text{m}^3$) (Willen 1959, Nauwerck 1963).

The phytoplankton data were computerized. Statistical evaluations and other data manipulations were conducted within the INFO data management system (Henco Software, Inc. 100 Fifth Avenue, Waltham, Mass.). By design, alternate east-west stations were sampled (e.g. 5 or 6, 10 or 11; Fig. 1) on various cruises in 1983 and 1984. This selection of sites were based on previous work which indicated that adjacent east-west sites were within homogenous areas of Lake Michigan. Beginning in 1985, a network of 11 fixed was sampled on each survey. In this report, to allow north to south comparisons, data from stations on an east to west axis were averaged to give one point. For example, data from Stations 22 and 23 were averaged to form one point on a north to south transect reported as Station 22 in Figures 1, 4 and 5.

Picoplankton are defined as rod or spherical shaped Cyanobacteria with a size less than $2\mu\text{m}$ (unicells or individuals within a colony). They were enumerated in the sample but are not included in this report because of very large numbers (e.g. 1983: 23,607 cells/ml, 89.4% of the total abundance), small biomass (e.g. 1.4% of the total biomass) and because of taxonomic uncertainties.

Zooplankton

A Wildco Model 30-E28 conical style net (62- μm mesh net; D:L ratio = 1:3) with 0.5-m opening (radius=0.25m) was used to collect a vertical zooplankton sample at at the same stations (Fig. 1 and Table 1) at which phytoplankton were collected during 42 cruises during the spring, summer, and autumn from 1983 to 1992. Only data from the unstratified spring period and the stratified summer period are presented here. Vertical tows were taken from 20m to the surface. Filtration volume was determined with a Kahl flow meter (Model 00SWA200) mounted 1/3 of the net diameter from one edge. Following collection, the net contents were quantitatively transferred to 500-mL sample bottles, narcotized with club soda and preserved with 5% formalin.

Enumeration of zooplankton followed Gannon (1971) while identification followed Stemberger (1979) and Edmondson (1959). The volume of each rotifer species was computed

by using the geometrical shape that most closely resembled the species (Downing and Rigler 1984). For each cruise, the length of at least 20 specimens of each rotifer species was measured. Width and depth were also measured on one date for each lake to develop length-width and length-depth ratios for use in the simplified formulas of Bottrell *et al.* (1976). Assuming a specific gravity of one, volume was converted to fresh weight and to dry weight assuming a ratio of dry to wet weight of 0.1 (Doohan 1973) for all rotifer species except *Asplanchna* spp. A dry weight/wet weight ratio of 0.039 was used for *Asplanchna* spp. (Dumont *et al.* 1975).

Because of the considerable variability in length and thus weight encountered in the Crustacea, the dry weights of Crustacea were calculated using length-weight relationships (Downing and Rigler 1984, Makarewicz and Likens 1979). Average length of crustaceans (maximum of 20 for each station) was determined for each station of each cruise. A comparison of calculated weights to measured weights of individual Crustacea in Lake Michigan suggested good agreement at the minimum weight range (Makarewicz 1988). The weight of the Copepoda nauplii and the veliger of *Dreissena* followed Hawkins and Evans (1979) and Sprung (1993).

The zooplankton data were computerized. Statistical evaluations and other data manipulations were conducted within the INFO data management system (Henco Software, Inc. 100 Fifth Avenue, Waltham, Mass.). As with phytoplankton, data from stations on a east west axis were averaged to give one point to allow north to south comparisons. All phytoplankton and zooplankton identifications and enumerations were performed by the Bionetics Corporation (1983-88), ASci (1989,1990) and Enviroscience (1991-92).

RESULTS AND DISCUSSION

Annual Abundance of Major Algal Groups

From 1983 to 1992, 543 species representing 145 genera comprised the offshore phytoplankton community of Lake Michigan (Tables 2 and 3). Common species for each year are presented in the Appendix (Tables A1 -A 10). Over 10 years, 39 common species and varieties accounted for 84.6% of the total abundance and 87.6% of the total biomass (Table 4).

The algal divisions with highest overall cell abundances were the Chrysophyta (973 cells/mL) and the Cyanophyta (891 cells/mL)(Table 5). The Bacillariophyta, however, contained the largest number of species (220 - >40% of all taxa identified)(Table 2) and by far the highest relative biomass (mean= 65.7%, range=14.6% to 85.7% of the total, Table 5). The number of

species of Chlorophyta was also high (133- 24% of all taxa identified), but the relative biomass was much lower (mean = 4.6%). In contrast, few Pyrrophyta species were present (11), but their relative biomass (mean = 6.1 %) was similar to that of the Chlorophyta (Table 5).

Time-trend patterns in relative biomass of algal divisions from 1983 through 1992 did not emerge from the data. Except for 1989, when the relative biomass of diatoms was unusually low (14.6%), relative biomass of diatoms dominated that of the other algal divisions ranging from 49.1% to 85.6%, with no distinct upward or downward trend (Fig. 2). In 1989 when diatom biomass was low, the relative and absolute biomass (Table 5, Fig. 2 and 3) of the Cyanophyta, Chlorophyta, Chrysophyta and Cryptophyta were greater than in previous and subsequent years. During the summer of 1989, abundance of diatoms was the second lowest recorded, while summer abundance of Chlorophyta was the highest over the 1983-92 period (Table 6).

Geographical Abundance and Distribution of Major Algal Groups

The far northern stations (Stations 57, 56 64 and 77) and the most southern stations (Stations 5 and 6) were sampled only in 1983 and 1984 (Fig. 1). Usually, mean algal biomass was high in northern Lake Michigan, decreased to a minimum at Station 41 (Fig. 4a), increased to Station 34 and then decreased southerly in Lake Michigan until Station 11. Biomass then increased slightly again at Station 6. This geographical pattern was determined by the diatoms (Fig. 5a). Pyrrophyta, Chrysophyta and Cryptophyta biomass was generally similar from north to south with the exception of the shallower Station 6 and the shallower or nearshore northern stations (77, 64, 57). At these shallower/nearshore stations, Chrysophyta biomass was higher. Pyrrophyta biomass was also higher at Station 6 but generally more variable at Stations 77, 64, and 57. Chlorophyta and Cyanophyta biomass varied little in the pelagic region of the lake but appeared lower at the southern Station 6. Chlorophyta biomass was also lower at the most northern Station 77.

In 1986, phytoplankton biomass increased from north to south (Fig. 4b) due to a bloom of Stenhanodiscus alpinus and S. transilvanicus in southern Lake Michigan (Fig. 6). The higher abundances in 1992 at Stations 41, 27 and 23 were also due to blooms of Stenhanodiscus alpinus, S. transilvanicus and Aulacoseira islandica (Fig. 6 and 7).

Dominant Species (1983-92)

Mean annual biomass of selected phytoplankton species are presented in Figs. 6-11. Monoranhidium contortum and an unidentified Green coccooid (Chlorophyta), Ochromonas sp. and Chromulina sp. (Chrysophyta), Rhodomonas minuta (Cryptophyta), Anacystis montana and Oscillatoria limnetica (Cyanophyta) were the numerically dominant non-diatoms in their respective divisions during the 1983-87 period (Table 7). For the 1988-92 period, a similar group of non-diatoms were numerically dominant with the exception of Monoranhidium minutum (Chlorophyta) and the Haptophyceae (Chrysophyta) (Table 8), which were more prevalent than during the earlier period.

Of the dominant Chrysophyta, Cryptophyta and Cyanophyta, Anacystis montana, Oscillatoria limnetica, Rhodomonas minuta were prevalent, if not dominant, in each year of the ten-year study (Tables A 1 -A10, Appendix). M. contortum was the dominant green algae in 1983 and 1984, but a "Green coccooid" was the numerically dominant green algae from 1985 through 1992 with the exception of 1991 when Monoranhidium minutum was the numerical dominant (Tables A1-A10, Appendix). Of the chrysophytes, Chromulina sp. and Ochromonas sp. were predominant and Dinobryon sociale was prevalent from 1983 through 1985. After 1985, Chromulina sp., Ochromonas sp. and D. sociale became less abundant while the Haptophyceae became progressively more prevalent in Lake Michigan (Fig. 11).

Numerically dominant diatoms in the 1983-87 period included Cyclotella comensis, Fragilaria crotonensis, Aulacoseira italica and A. islandica. On a biomass basis, Stephanodiscus alpinus, S. transilvanicus, S. niagarae and Rhizosolenia eriensis were predominant (Table 7). A similar group of diatoms were dominant in the 1988-1992 period with the exception of fewer R. eriensis present (Table 8). The dominance (biomass basis) of the various species of Stephanodiscus over the 1983-87 period was due to the unusually high biomass (over 45% of total biomass) of S. alpinus and S. transilvanicus in 1986 and 1987 (Fig. 6, Table 9).

The five-year averages presented in Tables 7 and 8 can be misleading, especially with the diatoms. Considering biomass, the dominant diatom species vary considerably from year. In 1983 and 1984, Tabellaria flocculosa, Fragilaria crotonensis, Rhizosolenia eriensis were dominant (Table 9). S. alpinus and S. transilvanicus were common species between 1983-85

but less prevalent than in 1986 and 1987 (Tables A1-A10, Appendix). Similarly, from 1988 through 1992, different species were predominant each year (Table 9). Thus for the IO-year period: Cyclotella comensis, Fragilaria crotonensis, Aulacoseira italica and A. islandica were numerically prevalent each year. On a biomass basis, a varying group of organisms were predominant each year that includes: Stephanodiscus alpinus, S. transilvanicus, S. niagarae, Rhizosolenia eriensis, Tabellaria flocculosa, Fragilaria crotonensis, Asterionella formosa and Aulacoseira islandica.

Fahnenstiel and Scavia (1987) sampled during the spring and summer at one offshore site near Grand Haven from 1982-84, which was near our deeper Station 23 (Fig. 1). Dominant diatoms observed by Fahnenstiel and Scavia (1987) included Aulacoseira islandica, Tabellaria flocculosa var. linearis, Tabellaria spp., Aulacoseira italica ssp. subarctica, and Fragilaria crotonensis with lesser amounts of Asterionella formosa. These diatom dominants were similar to the six most prevalent diatoms observed at our Station 23 in 1983 and 84 with the following exceptions: Asterionella formosa was not a dominant species at our site; Stephanodiscus alpinus (1983) and S. transilvanicus (1984) were co-dominants in the spring; and Rhizosolenia eriensis was prevalent in the summer of 1984 at our site.

Indicator Species

From 1983 to 1992, seven diatoms (numerical - Cyclotella comensis, Fragilaria crotonensis, Aulacoseira italica, and A. islandica; biomass - Stephanodiscus transilvanicus, S. niagarae and S. alpinus) were dominant. However, there has been a succession of dominant diatoms over the past ten years (Table 9). This is particularly noticeable when species are considered on a biomass basis. For example, the dominant diatom on a biomass basis was Tabellaria flocculosa in 1983 (17.0% of the total biomass), Rhizosolenia eriensis in 1984 (26.0% of the total biomass), Stephanodiscus niagarae in 1985 (10.6% of the total biomass), Stephanodiscus alpinus in 1986, 1987 and 1991 (35.5%, 43.0% and 20.9% of the total biomass, respectively), Asterionella formosa in 1988 (10.0% of the total biomass), Stephanodiscus transilvanicus in 1990 (16.3% of the total biomass) and Aulacoseira islandica in 1992 (22.0% of the total biomass). Except for Stephanodiscus niagarae, which is a eutrophic indicator species, and Aulacoseira italica subsp. subarctica, which is associated with alpine oligotrophic and mesotrophic lakes (Stoermer and Yang 1970), all these dominant species are associated with

mesotrophic conditions. As discussed previously, Stephanodiscus alpinus, a mesotrophic form, is becoming more prevalent in the lake.

Stoermer and Yang (1970), in a comparison of modern and historic records, reported that taxa characteristic of disturbed situations were rapidly increasing in relative abundance in Lake Michigan in the 1960's. In the nearshore area, a shift from oligotrophic forms to those which dominate under eutrophic conditions was evident. Occurrence of certain eutrophic species was also evident in offshore waters. During the period 1983- 1992, there was a shifting of diatom species, but it was shift in dominance from one mesotrophic indicator species to another, not a shift between trophic dominant types. From 1983-92, mesotrophic diatoms accounted for 47.2% of the total phytoplankton biomass (Fig. 12). Furthermore, the lack of a trend in the ratio of mesotrophic to eutrophic diatom species (Table 10) suggested that there was no change in trophic status during the 1983-92 period. Mesotrophic species of diatoms are the dominant forms in the pelagic region of Lake Michigan.

Historical Comparisons - Species Groups

The phytoplankton composition of the period 1983- 1992 was generally similar to that reported for 1962-1963 (Stoermer and Kopczynska 1967a) but some significant shifts in relative abundance of some species had occurred. Of the 15 common diatoms of the 1983- 1992 spring/summer period, 11 were mentioned by Stoermer and Kopczynska (1967a) as being found to a greater or lesser degree in southern Lake Michigan during 1962-1963. Diatoms common over 1983-1992 but not reported in the 1962-63 study included Cyclotella comensis, Nitzschia lauenburgiana, Rhizosolenia longiseta, and Stephanodiscus alpinus. In addition, Aulacoscira italica was said to occur sometimes at inshore locations in 1962, and Cymatopleura solea was present but only in small numbers.

During 1962-63, C. michiganiana was the dominant species in fall collections, followed by C. comta. The same species were present in reduced numbers in the spring collections. In August of 1970, C. michiganiana and C. stelligera were dominants in offshore waters (Holland and Beeton 1972). During the spring of 1977, Cyclotella spp. were common, but not dominant (Rockwell et al. 1980). By 1983, a dramatic decrease was observed in the abundances of both C. michiganiana and C. stelligera in the offshore waters (Table 11). These species met our definition of "common" only in 1990 and 1988, respectively. In contrast, Cyclotella comta was generally common during 1983-1992, and it was the only Cyclotella species to have an

aggregate biovolume greater than 1% of the total, but only then in some years. C. ocellata, a species generally associated with oligotrophic conditions and that was present in small numbers in 1962- 1963, likewise was usually present in small numbers during 1983- 1992. However, in 1984, 1986 and 1990 they were the fourth (27.1 cells/ml), seventh (15.3 cells/ml) and fifth (13.8 cells/ml) most abundant diatom, respectively, in the spring and summer assemblage. C. comensis, a species believed to be tolerant of higher nutrition and lower silica concentrations than most members of this genus, was not observed in 1970, but was common in all years 1983-1992 except 1985-1986. Biomass was especially high in 1983 (2.9 mg/m³), 1984 (5.2 mg/m³) and 1990 (3.6 mg/m³) (Figure 7).

Nitzshia lauenburgiana (not reported for 1962- 1963) and Cymatopleura solea (present in small numbers in 1962-1963) were common over the period 1983-1992 by virtue of their collective biomass being greater than 0.5% of the total. These species were only sporadically common, however. N. lauenburgiana was common in 4 of the 10 years, while C. solea was common in only 3 of 10 years, and not since 1987.

Rhizosolenia eriensis appears to have declined greatly since 1962. In May, 1962, relatively high populations (100 cells/ml) were observed in southern Lake Michigan (Stoermer and Koczyńska 1967a). Similarly, during May and June, 1970, mean abundances for offshore stations were 63 and 611 cells/ml, respectively (Holland and Beeton 1972). By June 1977, mean density of R. eriensis had declined to 28.7 cell/ml (Rockwell *et al.* 1980). During the periods 1983-1987 and 1988-1992, average whole lake abundances were only 7.5 and 3.3 cells/ml, respectively. Some sporadic higher abundances were observed. For example, an isolated bloom (110 cells/ml) was observed at Station 32 in August, 1984, and mean lake abundance in 1984 was 22.3 cells/ml. In 1990, a maximum of 81.8 cells/ml was observed at Station 19 in April, and the yearly average was 9.5 cells/ml. Over the period 1983-1992, there was clearly a decrease in annual biomass of this species (Fig. 6). R. longiseta, not reported in the 1962 and 1970, did appear in June, 1977, as a subdominant (Rockwell *et al.* 1980). This species represented 2.2% of total biovolume of the phytoplankton over the period 1983-1992, but it was common only during 1984-1986. From 1987 through 1992, few cells were found (Fig. 6).

Species of Stephanodiscus most commonly found in offshore waters in 1962-1963 were S. transilvanicus and S. niagarae. Some S. hantzschii were also reported from nearshore and harbor areas. No Stephanodiscus species were reported to be common in the 1977 collections (Rockwell *et al.* 1980). During 1983- 1992, S. alpinus, S. niagarae and S. transilvanicus were among the common species in each of the years. Although their species abundances were less than 1% of total cells each year (except for S. alpinus in 1986 (2.3%) and 1987 (1.2%)), their combined percentage of total algal biovolume exceeded 10% in 8 out of 10 years, and reached a maximum of 74.7% in 1986 (Fig. 13). Other small Stephanodiscus species became common by way of abundance for only 2 or 3 years during 1983-1992. Included were S. hantzschii (1986- 1988), S. minutulus (1986- 1987, 1991), S. parvus (1991 - 1992), and an unidentified species (1986, 1988).

Aulacoseira islandica was the dominant in offshore waters in 1962-1963 (Stoermer and Kopczynska 1967a), and it remained numerically important during 1983-1992. Also common during 1983-1992 (except 1989), however, was A. italica. Over the 10 years, A. italica and A. islandica were the third and fourth most abundant diatom, respectively, with an average of 30 and 27 cells/ml (Table 4). In 1983, 1987 and 1991, A. italica was the most abundant diatom, while A. islandica took that honor in 1986. Annual variation in abundance and biovolume of these two species was observed, but clearly greater biovolumes were found in 1991 and 1992 than during the previous eight years (Fig. 7).

Both Synedra ulna and S. acus were found in some abundance in 1963-1963 (Stoermer and Kopczynska 1967a), with S. ulna being the more common, but in 1977, S. acus was common throughout the southern basin (Rockwell *et al.* 1980). For the aggregated period 1983-1992, only S. ulna was common, but only as defined for biovolume. It has not been common in any single year except 1984 (average 2.9 cells/ml; maximum 23 cells/ml) and 1985 (average 2/6 cells/ml; maximum 33 cells/ml) (Fig. 8).

Dominant chrysophytes in 1962-63 were Dinobryon divergens, D. cylindricum and D. sociale (Stoermer and Kopczynska 1967a). Rockwell *et al.* (1980) reported them as dominant or subdominant offshore. D. divergens and D. sociale were common species during the 1983-92

spring and summer period (Table 4); however, considerable variability existed (e.g. Fig. 11).

For example in 1987, 1991 and 1992, neither of these two species were even common (i.e. having an abundance of > 0.5% of the total cells or > 0.5% of the total biovolume). D. cylindricum was common only in 1983 and 1984. The Haptophyceae were also predominant chrysophytes over the 1983-92 period, accounting for 6.8% of the total abundance and appear to be increasing in the lake over the 10-year study (Table 4, Fig. 11). Two flagellated chrysophytes enumerated in the 1983-1987 samples, but not identified, were tentatively identified in 1988 as Chromulina sp. and Ochromonas sp. (Fig. 8 and 11, Appendix A1). Numerically, these two species were the dominant chrysophyte species during the 10 year study.

Among the dominant and common cryptophytes between 1983-92 were C. erosa, Chroomonas norstedtii and Rhodomonas minuta. Stoermer and Kopczynska (1967b) reported these species as uncommon in Lake Michigan in 1962, but Munawar and Munawar (1975), Claflin (1975) and Rockwell et al. (1980) had reported C. erosa and R. minuta var. nannoplanktica to be abundant and perhaps increasing in number in the 1970s. For the 1983-1992 period, C. erosa was numerically the 4th most common cryptophyte, but on a biomass basis was the most important cryptophyte, surpassing many of the diatoms (Table 4, Fig. 9). Evaluation of the abundance of R. minuta in earlier (prior to 1962) studies was not possible because it was grouped into phytoflagellates, flagellates or simply Rhodomonas. However, between 1983-92 it was the by far the numerically dominant cryptophyte with a biovolume second only to C. erosa (Table 4, Fig. 9)

Anacystis montana was the dominant blue-green algae during the 1983-92 period (Table 4, Fig. 9). A. montana appears to be increasing within the pelagic region of the lake. Oscillatoria limnetica has also become more prevalent in the lake than during other studies. Ahlstrom (1936) and Stoermer and Kopczynska (1967a) listed Q. mougeotii as the only species of this genus abundant in their collections from 1962. Stoermer and Ladewski (1976) reported that Q. limnetica had generally increased in abundance in Lake Michigan in the early 1970s. Rockwell et al. (1980) observed that Q. limnetica was common throughout the basin in April and June and was especially abundant in September of 1977 at certain stations. During the 1983-92 spring/summer period, Q. limnetica (Fig. 9) was numerically (Table 4) the second most important offshore blue-green algae. However, except for a peak abundance in 1986, Q. limnetica generally declined from 1983 through 1992 (Fig. 10).

Historical Comparisons - Community Trends

In the spring of 1963, diatoms were overwhelmingly the most numerous phytoplankton group in southern Lake Michigan (Stoenner and Kopczynska 1967a). Similarly, in the spring of 1983-84 (Fahnenstiel and Scavia 1987) and in every year of our study (1983 to 1992) with the exception of 1989, diatoms were overwhelmingly dominant in the spring. The diatoms constituted from 69% (1983) to 95% (1986) of the total spring algae biomass.

During thermal stratification in the mid 1960s, diatoms were the dominant phytoplankton group (Schelske and Stoermer 1972). By the summers of the late 1960s and through the 1970s, blue-green and green algae became dominant (Rockwell *et al.* 1980, Bartone and Schelske 1982). Increased ambient phosphorus concentrations had allowed silica levels to be depleted by the summer, resulting in non-diatom species predominating (Schelske and Stoermer 1972). For example, in late July and August of 1976-78, blue-green and green algae accounted for over 50% of the total biomass (Bartone and Schelske 1982). In 1982, blue-green algae were still predominant in the summer accounting for 32% of the biomass, but by 1983 and 84 they accounted for less than 4% of the biomass at an offshore site near Grand Haven (Fahnenstiel and Scavia 1987). Instead phytoflagellates were prominent in the summer accounting for 91% and 68% of the summer biomass.

The lakewide data of this study support the concept of a shift in summer species composition. Similar to Fahnenstiel and Scavia (1987), we did not find the blue-green algae to dominate in the summer, but unlike Fahnenstiel and Scavia (1987), we did not observe the phytoflagellates to be prevalent in 1983 and 1984. Rather, the Pyrrophyta and the Bacillariophyta predominated. This difference in 1983 and 1984 in the data sets may be attributed to the difference in location of the Grand Haven site compared to the majority of the EPA sites. Our data clearly show that sites closer to shore or in shallower water, but still in the offshore region, have differing compositions of the major algal groups than the mid-lake sites that make up the majority of the EPA sites (Fig. 5). There was also considerable variability from year to year as to what phytoplankton groups were predominant in the summer: phytoflagellates in 1985 (22%), diatoms in 1986 (27%), phytoflagellates in 1987 (28%), Pyrrophyta in 1988 (31%), greens and chrysophytes in 1989 (47%), diatoms in 1990 (30%), diatoms and Pyrrophyta in 1991 (53%) and Pyrrophyta in 1992 (33%).

Fahnenstiel and Scavia (1987) suggested that at least two factors contributed to the shift in the summer epilimnetic phytoplankton community; nutrient supply and food web interactions. Nutrient supply as a cause does not appear likely. No significant changes in either ambient phosphorus or silica concentrations occurred during the spring or summer of the study period (Table 12). There is some evidence of a small decline in total phosphorus from 1981 to 1983 (Fig. 14). In particular, they suggest that changes in the Daphnia community (Evans and Jude 1986) are a likely cause of the phytoplankton compositional changes. The abrupt change in phytoplankton composition between 1982 and 1983 observed by Fahnenstiel and Scavia (1987) may be evidence of changes in higher trophic levels. With the increase in the Daphnia populations in the early 1980s in Lake Michigan, a change in the size composition of the phytoplankton would be expected. That is, with increasing abundance of large bodied Daphnia, large unicells, filaments and colonials should increase in the system. Or, as Daphnia populations decreased, small unicellular algae should predominate (Elsler and Goldman 1991). The data from 1983-1992 are consistent with the expected shifts in predominant cell sizes. In 1983 and 84, when large Daphnia predominated, small unicellular algae accounted for 29% and 28% of the total phytoplankton biomass, respectively. After 1984, when Daphnia abundance decreased, the percent biomass of unicellular algae increased to 53% (Fig. 15). For the next eight years unicellular algae biomass fluctuated from 40-54%, which corresponds with the reduced populations of large Daphnia in the lake.

Historical Changes: Trophic Status, Community Abundance and Size Distribution

Based on the classification scheme of Munawar and Munawar (1982), which utilizes the mean phytoplankton biomass as an indicator of trophic status, Lake Michigan offshore waters (1983-92 mean=0.54 g/m³) would be classified as oligotrophic (0.5- 1.0 g/m³). However, the number and high biomass of mesotrophic indicator diatom species, suggests a mesotrophic status. Similarly, Tarapachak and Stoermer (1976) classified Lake Michigan as mesotrophic based on the diatom composition. This agrees well with the 1976 assessment of Barton and

Schelske (1982) who believed that the open waters of Lake Michigan in 1976 to be either in the upper range of oligotrophic or mesotrophic based on particulate phosphorus concentration.

A comparison of abundance trends over the entire lake was not possible because of the lack of comparable offshore data prior to 1983. In Figure 16 are plotted the 1962-63 and the 1976-77 data of Stoermer and Kopczynska (1967a and b) and Rockwell *et al.* (1980), which are representative of the southern portion of the lake along with data from this study. Only a range of abundance is available for 1962-63, while the mean, standard error and range are plotted for the other data. Although a mean is not available, it is apparent that phytoplankton abundance increased between 1962-63 to 1976-77. From 1976 to 1983 and 1985, where data for April through November was available, abundance was not significantly different ($P > 0.05$) (Fig. 16a). Considering only the spring and summer data (Fig. 16b), there appears to be a slight downward, but not significant ($P = 0.153$) trend in abundance from 1983 onward.

Although abundance has not significantly changed during the period of study, a fluctuation in the relative importance of different size fractions has occurred (Fig. 17). The springtime relative biomass of filaments, colonial and large unicell algae ($> 50\mu\text{m}$) decreased from 50% during 1983-1985 to less than 25% of the total biomass in the spring of 1986 and 1987. Small unicellular algae ($< 50\mu\text{m}$) increased to over 75% of the total biomass during the same time period. After 1987, the small relative biomass of unicellular algae decreased and the filamentous colonial and large unicellular algae increased within the system. The relative importance of filamentous algae increased from 9.9% in 1990 to over 25% in the spring of 1991 and 1992, while the colonial and large unicell fraction decreased. These changes in size structure of the phytoplankton community may (Brooks *et al.* 1984) or may not (Evans 1992) be related to changes in zooplanktivory caused by the changing composition of the predator population. *Daphnia*, which are often correlated with changes in phytoplankton biomass, are not present in the spring in Lake Michigan where our samples were collected. Thus the changes observed in size composition are most likely associated with nutrients and physical factors (day length, mixing depth, etc.), such as temperature (Bartone and Schelske 1982). However, these changes in the size distribution during the spring are not correlated with any changes in ambient levels of silica, phosphorus or temperature since 1983 (Table 12).

During the 10 year study period, major changes occurred in the summer zooplankton population (This study). In particular, populations of large species of *Daphnia* bloomed and

crashed in response to planktivory by alewife and perhaps Bythotrephes cederstroemii. Little or no change in the relative biomass of filaments, colonial algae, and large unicells occurred (Fig. 15). Small unicells did increase immediately after the large Danhnia pulicaria decreased, but no further changes in the phytoplankton community were correlated with extensive changes in the zooplankton community.

Scavia et al. (1986) concluded that the summer plankton community of Lake Michigan is controlled largely by predation. As mentioned earlier, there is some evidence that the size composition of the summer phytoplankton changed in 1985 to a greater percentage of small unicells (Fig. 16) as large Danhnia became less prevalent. Modeling of the food web predicts a return to a plankton community similar to that of the 1970s with Diantomus-dominated zooplankton and a substantial filamentous blue-green component under a scenario of increasing invertebrate predation by a new zooplankton species for Lake Michigan, Bythotrephes cederstroemi (Scavia et al. 1988). In fact, the relative importance of filamentous algae increased from 9.9% in 1990 to over 25% in the spring of 1991 and 1992, while the colonial and large unicell fraction decreased. While composition has changed the total biomass of algae was not affected by food-web changes, which is similar to the conclusion of Lehman (1991).